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DIGESTIVE SYSTEM AND ASSOCIATED ORGANS IN THE ADULT AND PUPAL MALE DORYLINE ANT *AENICTUS GRACILIS* EMERY (HYMENOPTERA: FORMICIDAE)[1]

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Abstract.—This paper presents the first description of the anatomy and histology of the alimentary tract, the postpharyngeal glands, the salivary glands, the Malpighian tubules, and the mandibular glands in the male adult and pupa of the Old World doryline ant, *Aenictus gracilis.* The alimentary tract consists of the cibarium, the buccal tube, the infrabuccal chamber, the pharynx, the oesophagus, the cardiac valve, the ventriculus, the pylorus, the intestine, the rectal valve and the rectum. In the adult the infrabuccal chamber lies posterior to its usual position in ants under the posterior floor of the buccal tube and the anterior pharynx, while the pupa has a recess where the infrabuccal chamber is usually present. The pharynx is divisible into a broad anterior, an indented middle, and a tubular posterior region into which the postpharyngeal glands open. The epithelium of the pharynx has flattened cells in the adult and low columnar cells in the pupa. The intima of the postpharyngeal glands and ducts bears long hair-like projections. Maxillary glands are absent. The epithelium of the oesophagus has small folds in the pupa and the lumen is wider than in the adult. The continuation of the oesophagus into the ventriculus is the cardiac valve. A crop and a proventiculus are absent. The ventriculus has a dorsal concavity toward its posterior half. The ventricular epithelium of the adult consists of digestive and regenerative cells. In the pupa the ventricular epithelium has disintegrating and regenerating regions. The regenerating digestive cells are of three distinct types that represent stages in the maturity of the epithelium. The pylorus is internally divided into an anterior region where the 18–20 Malpighian tubules enter, and a posterior region. The posterior extension of the intestine into the rectum is the rectal valve. The inner wall of the rectum has 3 rectal pads. The very small salivary glands are of the simple branched acinar type, and their ducts have a tortuous cuticular lined lumen. The mandibular gland consists of about 12 pyriform cells and a reservoir. Comparisons made with the other Old World and New World species previously described have revealed features of phylogenetic importance that lend support to the concept of the triphyletic origin of the dorylines.

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The study of the morphology, anatomy and histology of male ants is of particular importance because as Janet (1902) recognized, they are the least specialized of all of the nest forms and most wasp-like in appearance. This wasp-like appearance offers evidence that ants evolved from wasp-like insects. A review of the literature on the anatomy of ants indicates that the males have been studied only in a very few of the numerous genera and species. These studies have brought to light anatomical and histological differences in the organs and systems at the subfamily, generic, and in some even at the species level, that are of phylogenetic importance. As stated by Wheeler (1910) the males are stable in structure and, if more readily obtainable, would be valuable in the taxonomy of the group.

The digestive system of male ants was first described by Meinert (1861) in a formicine, *Formica rufa,* and a myrmicine, *Myrmica ruginodis.* He illustrated differences in the structure of the proventriculus in these two species; this was the first indication of the importance of this organ as a basis for determining phylogenetic relationships of various genera of ants. Forel (1878) and Emery (1888) used the diverse features of the proventriculus for taxonomic purposes. Descriptions of the anatomy of the digestive system that followed were those of Janet (1902) in the gaster of a myrmicine, *Myrmica rubra,* Mukerjee (1926) in an Old World doryline, *Dorylus labiatus,* Marcus (1953) in a dolichoderine, *Dorymyrmex emmaericaellus.* A comprehensive and comparative study of the proventriculus in ants was made by Eisner (1957),who formulated a phylogenetic dendrogram in which he placed the dorylines parallel to the poneroid complex but with a different origin than had been postulated for other groups of ants. More recent observations of this organ are those of a ponerine, *Rhytidoponera metallica,* (Hagopian 1963), and two species of myrmicines, *Myrmica rubra,* (Trachimas 1967), and *Solenopsis invicta* (Buren 1972) = *S. saevissima richteri* Forel (Tice 1967). The present investigation has revealed the absence of a crop and a proventriculus in both the adult and pupa of the male of *Aenictus gracilis.* Prior to Eisner's paper (1957), Brown (1954) in a study on the phylogeny of ants stated that the precise affinities of the dorylines are unknown, and it is possible that they are diphyletic in origin. Gotwald (1969) in his exhaustive study of the mouthparts of 104 species of ants revealed distinct differences between the New World and Old World dorylines, and in the Old World doryline genera between *Dorylus* and *Aenictus.* Thus he advocated a triphyletic origin for the dorylines separating the tribes Dorylini, Aenictini, and Ecitonini from one another. Schneirla (1971) considered dorylines as monophyletic in origin on the basis of functional and behavioral evidence.

In addition to the above mentioned papers on the digestive system of ants, three other reports have been published on the internal anatomy of the

New World doryline workers (Whelden 1963, Gotwald 1971, Gotwald and Kupiec 1975).

The present work is the first comprehensive anatomical and histological description of the digestive system of the male adult and pupa of the Old World doryline *Aenictus gracilis*. Comparisons are made with those of the other dorylines previously described.

Materials and Methods

The 12 male adults, and the 12 pupae at an advanced stage of development used in this study were collected by the late Dr. T. C. Schneirla from a bivouac on an eastern mountain slope above Dumaguete City, Negros Island, Philippine Islands, in 1962. The specimens were preserved in 70% ethyl alcohol. Each specimen was mounted on paraffin in a Syracuse watch glass and dissected under 70% ethyl alcohol. Whole mounts of organs were prepared by Lynch's precipitated borax-carmine method (Galigher and Kozloff 1971), and specimens for histological study were processed by a double infiltration technic (Trombetta and Forbes 1977). Frontal, sagittal, and transverse serial sections were cut and stained with Harris' haematoxylin, counterstained with eosin and mounted in euparal. Drawings were made with the aid of a camera lucida and a B & L trisimplex microprojector.

Anatomy of the Digestive System

The anteriormost part of the alimentary tract in the adult and pupa is the cibarium that leads into a wide dorsoventrally compressed buccal tube. The thin-walled buccal tube is broader anteriorly, and in the adult the posterior floor opens into an elongated, flattened infrabuccal chamber that extends beneath the anterior pharynx (Fig. 1). In the pupa an irregular recess is located beneath the anterior floor of the buccal tube, where the infrabuccal chamber is normally found in ants (Fig. 2). The pharynx that continues is distinguishable into a broad anterior, an indented middle, and a tubular posterior region. The lateral margins of the anterior region become progressively more sclerotized posteriorly into the indented region. Bundles of muscle fibers extend from the dorsal surface of the anterior region to the inner, anterior surface of the head capsule. Arising from the dorsolateral wall on each side of the posterior region of the pharynx is a duct that divides into numerous branching, and convoluted tubular postpharyngeal glands. These glands extend anteriorly as far as the buccal tube and laterally and posteriorly over the front part of the brain. The posterior end of the pharynx continues as a narrow oesophagus passing between the brain dorsally and the suboesophageal ganglion ventrally and through the neck, the thorax, and the petiole into the gaster. In the gaster, about the beginning of the 4th

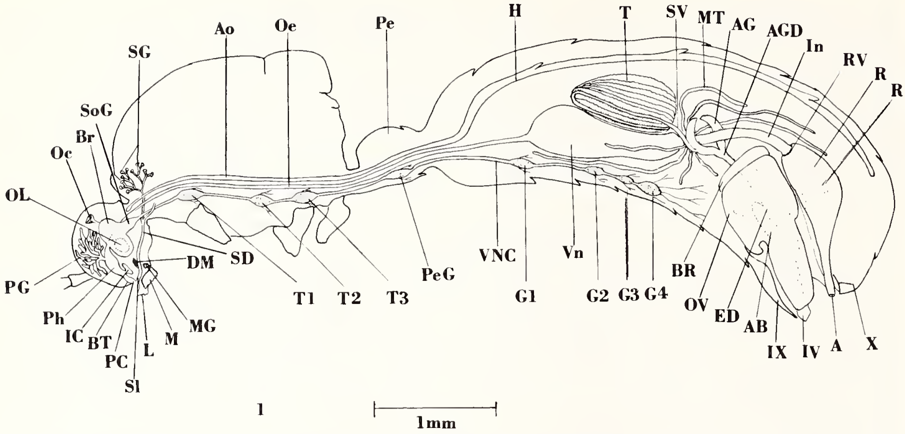
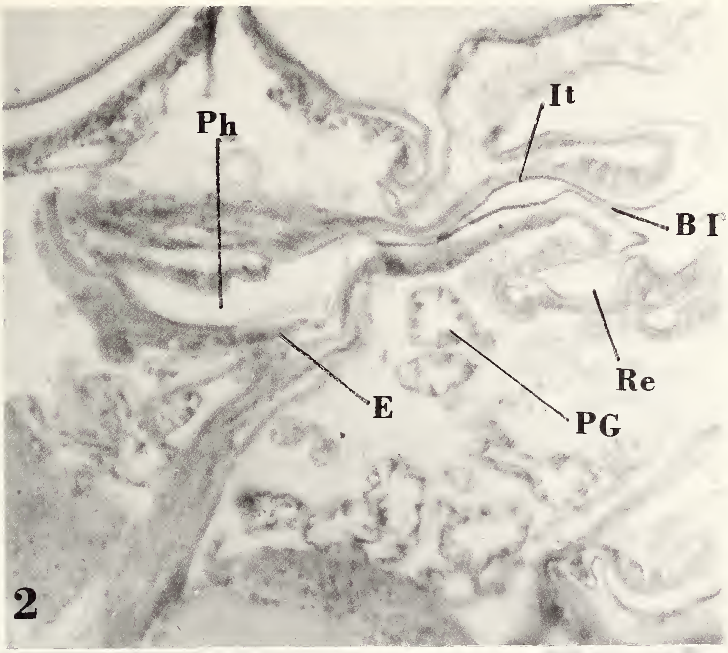


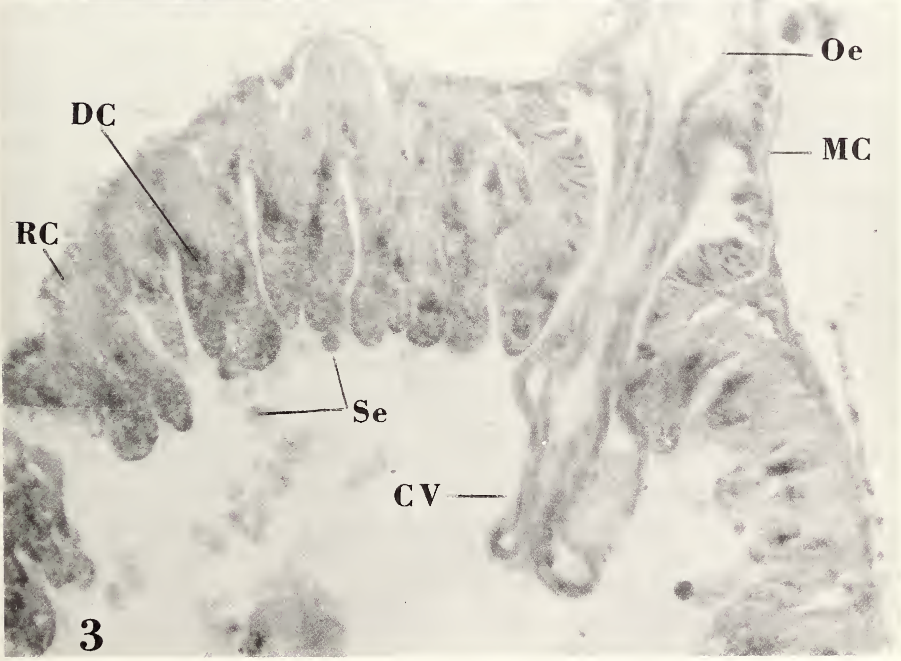
Fig. 1. Diagram of a lateral dissection of the adult male of *A. gracilis*.

ABBREVIATIONS

A, anus; AB, aedeagal bladder; AG, accessory gland; AGD, accessory gland duct; Ao, aorta; B, basal cell layer; Br, brain; BR, basal ring; BT, buccal tube; CV, cardiac valve; DC, DC1, DC2, DC3, digestive cells; DM, dilator muscle; Dt, ductule; E, epithelium; ED, ejaculatory duct; Ey, lower part of the eye; G1, G2, G3, G4, gastric ganglia; GC, glandular cell; H, heart; I, inner cell layer; IC, infrabuccal chamber; In, intestine; It, intima; IV, inner genitalic valve; L, labium; Lu, lumen; M, mandible; MC, muscle coat; MG, mandibular gland; MT, Malpighian tubule; Oc, ocellus; Oe, oesophagus; OL, optic lobe; OV, outer genitalic valve; PC, preoral cavity; Pe, petiole; PeG, petiolar ganglion; PG, postpharyngeal gland; Ph, pharynx; R, rectum; RC, regenerative cell; Re, recess; RP, rectal pad or gland; Rv, reservoir; RV, rectal valve; SD, salivary duct; Se, secretion; SG, salivary gland; Sl, salivarium; SoG, suboesophagal ganglion; T, testis; T1, T2, T3, thoracic ganglia; Vn, ventriculus; VNC, ventral nerve cord; IX, 9th abdominal sternum; X, 10th abdominal tergum

abdominal segment, the oesophagus projects into the ventriculus and forms a cardiac valve. The ventriculus is the largest organ of the alimentary tract and extends to the middle of the 5th abdominal segment. Its anterior half is broadly rounded, the posterior half is narrower and has a dorsal concavity. The distal end of the ventriculus is constricted at the junction with the intestine. The proximal region of the intestine is the slightly wider pylorus where the Malpighian tubules enter. The rest of the intestine occupies the 5th through the 7th abdominal segments, and about halfway along it bends dorsally, increases slightly in diameter, projects into the rectum, and forms a rectal valve. The rectum is a thin-walled, pyriform sac in the 8th and the 9th abdominal segments and lies above the genital chamber. The inner wall of the anterior region of the rectum has 3 rectal pads; two are lateral and one is ventral in position. The rectum tapers to the anus that opens to the outside on the ventral surface of the 10th tergum.





Figs. 2–3. 2. Photomicrograph of a sagittal section of the head of the male pupa to show the buccal tube and pharynx. ×450; 3. Photomicrograph of a sagittal section of the cardiac valve and anterior part of the ventriculus of the adult male. ×400.

Histology of the Digestive System

The epithelium of the buccal tube and the infrabuccal chamber is composed of a single layer of small, squamous cells with very small, centrally located nuclei and is lined by an intima. The intima on the roof of the buccal tube is thinnest anteriorly, thickest, transversely ridged and weakly sclerotized in the midregion, and thinner and more sclerotized with small hair-like processes in the posterior region. The intima on the floor and in the infrabuccal chamber is very thin. The epithelium is not surrounded by a muscle coat in this region. In the pupa, the epithelium of the buccal tube is composed of cuboidal to low columnar cells. The intima throughout this region is uniformly thicker than that in the adult and has hair-like processes along the floor pointing toward the preoral cavity.

The epithelium of the pharynx is composed of a single layer of flattened cells with oval nuclei. The intima in the proximal part of the anterior region on the roof and floor is thick, sclerotized and forms plate-like layers, and sharp, hair-like processes on the floor project forward. Muscles are present only on the roof of this region and consist of the oblique fibers that extend to the head capsule and some longitudinal bundles that extend from front to back. In the distal part of this anterior region, the lateral walls are curved dorsally, and here the intima is more sclerotized than on the roof and floor. There are three bundles of longitudinal muscle fibers separated by two bundles of the oblique fibers. In addition, on the ventral side transverse muscle fibers extend between the ventrolateral margins of the pharynx. The middle indented region has heavily sclerotized, sharp, dorsal extensions of the lateral margins and the lumen is U-shaped. The muscles here consist of longitudinal and the oblique fibers in the dorsal concavity and transverse fibers that connect the dorsolateral arms. The distal region of the pharynx has an intima that is thicker along the floor. The muscles in this region are a continuation of those of the indented region. In the pupa, low columnar cells form the epithelium of the pharynx and the intima is thin and not sclerotized.

The postpharyngeal glands have a single-layered cuboidal epithelium. The cytoplasm is acidophilic, granular, and vacuolated, and the small oval nuclei are basally located. The glands and ducts are lined by a thin intima bearing long, hair-like projections. The lumina are devoid of any secretion. In the pupa the epithelium of these glands is folded and composed of low cuboidal or squamous cells with spherical or flattened nuclei. The hair-like projections of the intima are less numerous than in the adult, and the lumen is more spacious (Fig. 2).

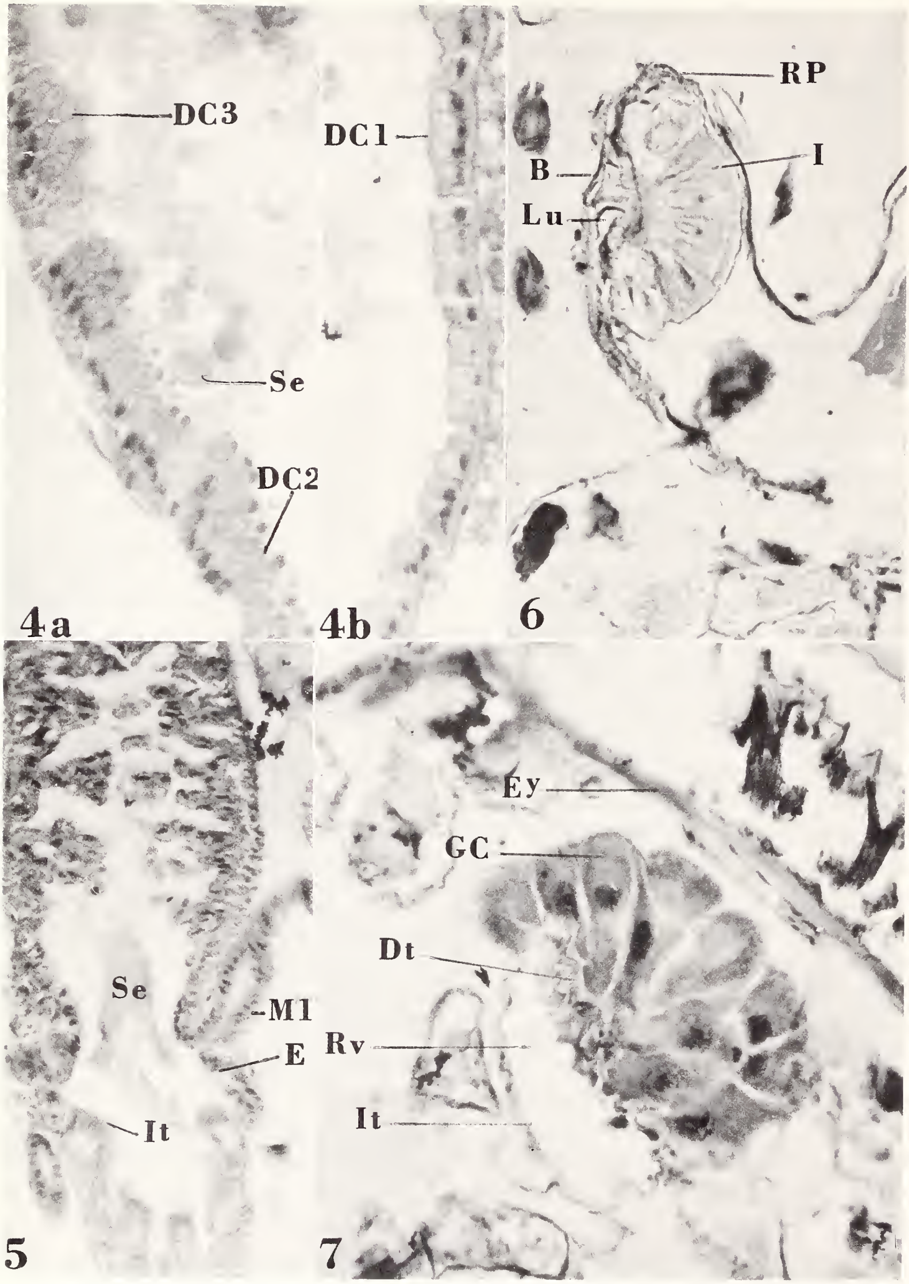
The oesophagus has a low cuboidal epithelium, longitudinally folded inward to form 4 or 5 ridges, and covered by a thin intima. Toward the distal end the folds are reduced in height and the lumen is wider. The muscle coat is composed of inner longitudinal fibers, some extending into the epithelial folds, and outer circular fibers. Toward the distal end a layer of 1 or 2 longitudinal fibers is present around the circular layer. In the pupa epithelial folds are small and the lumen is wider.

In the adult and pupa the cardiac or stomodaeal valve has a reflected, low cuboidal epithelium (Fig. 3). The intima terminates at the base of the outer walls of the valve. No muscle fibers are present within the valve.

The epithelium of the ventriculus is composed of large columnar, digestive or secretory cells, and small pyramidal, regenerative cells (Fig. 3). Some of the digestive cells are tall and narrow and their free ends are swollen and globular. In many of these cells the nucleus has migrated upward to the globular region and is compact and irregular in shape. The cytoplasm is neutral in its staining reaction and has basophilic granules throughout. In some of these cells granules are concentrated toward the free margin. The globular ends of some have ruptured and discharged the granular material into the lumen of the ventriculus. The regenerative cells are widely scattered clusters of a few cells each. They have a basophilic cytoplasm and oval nuclei. The muscle coat surrounding the epithelium consists of an inner circular and an outer longitudinal layer that are about equal in thickness; the fibers of the outer layer are widely separated. Sections of the pupal ventriculus show that the epithelium of the mid and posterior regions is disintegrating, while that of the anterior and some of the midregions is regenerating (Figs. 4a and b). The disintegrating cells are columnar in shape, and their basally located nuclei are irregular in shape. The cytoplasm is filled with fine, basophilic granules and small vacuoles. The free surfaces of the cells are broken and the cytoplasmic material is released into the lumen. The regenerating cells in the anterior ventral region are low, broad cells with basally located, compact, spherical nuclei. The cytoplasm is finely granular and homogeneous throughout with a thin compact layer of granules just underneath the free surface. On the anterior dorsal region the cells are tall, narrow columnar cells and the free surface is swollen and contains an acidophilic secretion. In the midregion these cells on the ventral side are also short and broad while those on the dorsal side are tall and narrow. The cytoplasm of these cells in this region is uniformly granular, and the nuclei are basally located and ellipsoidal in shape.

In the adult and pupa the pylorus is divided into anterior and posterior portions by an inward fold of the epithelium (Fig. 5). Low columnar cells in the anterior region, taller and wider cells over the fold, and small cuboidal cells in the posterior region form the epithelium. The cytoplasm is compact, finely granular and acidophilic. The intima, seen in some sections just behind the entrance of the Malpighian tubules, is always more distinct over the epithelial fold. Inner circular and outer longitudinal fibers form the muscle coat.

The intestine in the adult and pupa has a folded, cuboidal epithelium



Figs. 4–7. 4. Photomicrographs of sagittal sections of the ventriculus of the male pupa. ×325. a. Dorsal wall and b. Ventral wall; 5. Photomicrograph of a sagittal section of the ventriculus and pylorus of the adult male. ×215; 6. Photomicrograph of an oblique section of the rectum of the adult male to show a rectal pad. ×225; 7. Photomicrograph of a sagittal section of the head of the adult male to show the mandibular gland. ×300.

covered by a distinct intima. The cells of the folds are taller, but the folds diminish in height and disappear toward the distal region. The lumen contains a finely granular basophilic secretion. An inner very thin layer of longitudinal muscle, a middle compact layer of circular muscle, and an outer layer of longitudinal fibers form the muscle coat. The epithelium and the muscle coat project into the rectum and form a rectal valve. Here, the circular muscle layer is thick and forms a sphincter.

In the adult and pupa the rectal epithelium is a single layer of flattened squamous cells covered by an intima. The nuclei are spindle-shaped. The muscles consist of a single layer of circular fibers and scattered longitudinal fibers. A heavier band of circular muscle surrounds the anus and forms the anal sphincter. Each rectal pad is composed of an inner tall, columnar layer and a basal cuboidal layer separated by a lumen (Fig. 6). The inner columnar layer of cells is a continuation of the epithelium of the rectum, and the transition from the squamous to columnar cells is abrupt. The cytoplasm of the inner and the basal cells is vacuolated and has basophilic granules. The inner cells are faintly striated toward the lumen between the cell layers. The intima covering the rectal pad is slightly thicker than that lining the rectum.

The adult and pupa have 18 to 20 long, slender Malpighian tubules that open into the anterior end of the intestine at the pylorus (Fig. 5). They lie coiled around the intestine and the accessory glands of the reproductive system, some extending anteriorly as far as the proximal region of the ventriculus and some posteriorly as far as the rectum. The epithelium is composed of a layer of 4 or 5 large cuboidal cells with a striated free surface. The large nucleus has a prominent nucleolus and chromatin material. The cytoplasm has coarse basophilic granules. The lumen is filled with a neutral, granular secretion.

The salivary glands are microscopic in size and are located in the lateral regions of the prothorax (Fig. 1). In the early stages of this work when the organs and systems of the adults and pupae were dissected and studied as whole mount preparations, the salivary glands and the gland ducts were not recognizable. The salivary duct in the head and the lateral ducts in the neck region were found. Examination of the serial sections did reveal the glands and their ducts, and the following description is based on these observations. The glands are simple branched acinar glands and the acini are clustered or distributed singly and interspersed in the fat cells. Each acinus consists of a layer of pyramidal cells around a small lumen lined by a thin intima and built on a distinct basement membrane. The cytoplasm of these cells in the adult is homogeneous and basophilic with some vacuoles, while in the pupa it is more vacuolated with large basophilic granules. The nuclei are spherical or oval and centrally or basally located. The collecting ducts, the lateral salivary ducts and the common salivary duct are composed of cuboidal cells with ellipsoidal nuclei. The lumen of the salivary ducts, lined with a heavy intima that has annular thickenings, is tortuous and forms U-shaped loops within the cells of the ducts. The common salivary duct proceeds below the brain and opens into the salivarium which is situated between the hypopharynx and the labium. Where the salivary duct opens into the salivarium a dilator muscle extends from the roof of the duct to the ventral wall of the hypopharynx.

The adult and pupa have a pair of mandibular glands located at the bases of the mandibles (Fig. 1). Each consists of a glandular portion and a reservoir. The glandular portion is hemispherical with about 12 pyriform glandular cells with intercellular spaces between them (Fig. 7). These intercellular spaces are lined with a thin cuticle. The glandular portion is encased in a thin membrane. The cells open by small ductules into the thin-walled reservoir, and the intercellular spaces converge toward the reservoir. A short duct leading from the reservoir opens laterally at the base of the mandible. The cytoplasm of the glandular cells is homogeneous with fine basophilic granules. The spherical or oval nucleus has a prominent nucleolus and coarse chromatin granules. The membrane surrounding these cells is composed of a layer of squamous cells covered by a thin cuticle. The wall of the reservoir and the duct has a layer of squamous cells lined by a wrinkled intima.

Discussion

The adult has an infrabuccal chamber while the pupa has an anterior recess in that region. The epithelium of the buccal tube and the pharynx consists of squamous cells in the adult and cuboidal or low columnar cells in the pupa. The pharynx of *A. gracilis* resembles in structure the Old World doryline *Anomma wilverthi* (Bugnion, 1930), and in general histology the New World *Eciton* (Whelden, 1963) and *Cheliomyrmex morosus* (Gotwald, 1971). However, variations are seen in the arrangement of spines along the inner surface.

The epithelium of the postpharyngeal glands is folded in the pupa of *A. gracilis* and not so in the adult.

The oesophageal epithelium of the pupa of *A. gracilis* has smaller folds and the lumen is wider when compared to the adult. The long, acute spines reported in the queens and workers of two species of *Eciton* (Whelden, 1963) are absent here.

A crop and proventriculus generally present in ants between the oesphagus and ventriculus are absent in *A. gracilis* and in the Old World *D. labiatus*. Eisner (1957) described the proventriculus in *E. hamatum* as degenerate. Whelden (1963) has reported a difference in the position of the small crop in queens and workers of two species of *Eciton* (*hamatum* and *burchelli*), and the presence of a small proventriculus in both species. In the worker of *C. morosus* the crop and ventriculus lie juxtaposed and are connected by a reduced membranous proventriculus (Gotwald and Kupiec, 1975). There is no mention of a cardiac valve at the posterior end of the oesophagus in *D. labiatus* (Mukerjee, 1926). A simple cardiac or stomodaeal valve is reported to be present in *E. hamatum* (Eisner, 1957) and in *C. morosus* (Gotwald, 1971). In the adult and pupa of *A. gracilis* the posterior end of the oesophagus continues into the ventriculus and forms a cardiac valve; this valve is shorter in the pupa.

The ventriculus of the adult and pupa of *A. gracilis* resembles in general form that of the ponerine male, *Rhytidoponera metallica,* (Hagopian, 1963) in having a dorsal concavity in its posterior half. The New World doryline *C. morosus* worker has a tubular posterior portion that is referred to as the pre-Malpighian tubule tract (Gotwald, 1971). This has not been reported in any of the other species described (Mukerjee, 1926; Whelden, 1963). The ventricular epithelium of the adult of *A. gracilis* is composed of large columnar digestive cells and small, scattered, pyramidal regenerative cells. In the pupa, however, three types of digestive cells, each restricted to a region of the ventriculus, were recognized, and these represent stages in the maturity of the epithelium.

A pylorus that is divided into anterior and posterior portions by an inward fold of the epithelium is present in the adult and pupa of *A. gracilis.* This is indicated as a pyloric constriction in *D. labiatus* (Mukerjee, 1926). Such a pylorus is not reported in the New World species described (Whelden, 1963; Gotwald, 1971).

The intestine is a tube of uniform diameter in all ants described. In *D. labiatus,* however, it is reported to be divisible into an anterior narrow ileum and a posterior broader colon (Mukerjee, 1926).

At the junction of the intestine and the rectum a rectal valve with a sphincter is present in the adult and pupa of *A. gracilis.* A structure comparable to this has not been reported in any of the other dorylines described (Gotwald, 1971; Mukerjee, 1926; Whelden, 1963). There seems to be no consistency in the number of rectal pads or papillae; small rectal glands in *D. labiatus* male (Mukerjee, 1926), usually 3 and rarely 6 in *Eciton* workers and frequently 6 and infrequently 3 in *Eciton* queens (Whelden, 1963); 2 lateral papillae in the worker of *C. morosus* (Gotwald, 1971). The present investigation revealed the presence of 3 rectal pads in the adult and pupa of the male, two lateral and one ventral.

Maxillary glands situated on either side of the infrabuccal chamber and opening into the posterior part of the buccal tube have been reported in the male ponerine ant, *R. metallica* (Hagopian, 1963), in the queens and workers of the two species of the New World doryline, *Eciton* (Whelden, 1963), and in the workers of a New World doryline, *C. morosus* (Gotwald and

Kupiec, 1975). These glands are not present in adults and pupae of the male *A. gracilis.*

There are 18–20 Malpighian tubules in the adults and pupae of the male of *A. gracilis.* Mukerjee (1926) has reported the presence of numerous tubules in the male of *D. labiatus.* Analysis of the Malpighian tubule count made by Gotwald (1971) indicates that the range in number of tubules in workers is less species specific. However, the mean numbers of tubules are distinct for several species and he assumes that they could be correlated with the body size; a higher mean for the larger *Labidus* species, and a lower mean for the smaller *Neivamyrmex* species. The present count of 18–20 for one of the smallest of the dorylines, *Aenictus,* does not support Gotwald's assumption.

Salivary glands and gland ducts in the adult and pupa of *A. gracilis* are very small and interspersed in fat cells. The glands are simple branched acinar glands, and the ducts are typical in being straight with a tortuous lumen. In the other dorylines described these glands are of different types; short, thick, and branched tubules in *Eciton* workers and queens (Whelden, 1963), and small cylindrical lobes in workers of *C. morosus* (Gotwald, 1971).

Whelden (1963) reported much variation in shape and in size of the mandibular gland and the reservoir in the two species of *Eciton.* In the males of these species he describes the posterior end of this gland as being frequently bifurcate, the two branches passing one above, the other below the optic nerve. The number of secretory cells in these glands varies from 100 to 1400. The mandibular gland in *C. morosus* (Gotwald and Kupiec, 1975) is composed of a few irregularly-shaped cells with distinct nuclei; a reservior was not reported. The glandular portion of *A. gracilis* resembles in all respects that of the ponerine, *R. metallica,* (Hagopian, 1963). *A. gracilis* has a reservoir into which the cellular ductules and the intercellular spaces of the glandular portion open.

Gotwald and Kupiec (1975), analyzing the existing information on the morphology, behavior and geographical distribution of the doryline tribes indicate that the subfamily Dorylinae as presently constituted, is triphyletic. The three lineages are the Ecitonini-Cheliomyrmecine, the Dorylini, and the Aenictini. They advocate the retention of the subfamily Dorylinae to include the tribe Dorylini and make a case for the creation of a subfamily Ecitoninae already introduced by Brown (1973) to include the tribes Ecitonini and Cheliomyrmecini. The status of Aenictini, they conclude, remains to be determined by further investigation.

The present investigation of the anatomy and histology of the digestive system has brought to light several features of phylogenetic importance. In the absence of a crop, a proventriculus, and maxillary glands, *Aenictus* is distinctly different from the New World forms. The presence of a dorsal concavity in the posterior half of the ventriculus, the pylorus internally divided into anterior and posterior portions, and the presence of a rectal valve with a sphincter are the unique features exhibited in the digestive system of *Aenictus*. These structures lend support to the elevation of the tribe Aenictini to a subfamily rank, and add to the concept of the triphyletic origin of the dorylines.

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